

New species of deep-sea gastropods from the Indo-West Pacific Region (Gastropoda: Vetigastropoda: Seguenzioidea: Calliotropidae) with a geologic and biogeographic perspective

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ABSTRACT

This paper identifies the biogeographic realm of Wallacea as a center of deep-sea (>200 m) endemism in the basal gastropod family Calliotropidae Hickman and McLean, 1990. Six new medium- to large-shelled species are described from Sulawesi: *Calliotropis bukabukaensis*, *C. tominiensis*, and *C. new species* from >1000 m in the Gulf of Tomini and *C. tabakuensis*, *C. locolocoensis*, and *C. lamuluensis* from the > 988 m in the Gulf of Bone. Two additional large-shelled species are described: *C. enantioserrata* from >1000 m on the eastern Australian slope in the northern Tasman Sea and *C. andamanensis* from 500 m in the Andaman Sea off the west coast of Thailand. Previous descriptions and records of *Calliotropis* species in Indonesia are from the margins of Wallacea—the Makassar Strait and Islands in the Banda Arc, notably Kai, Tanimbar, and Timor. When calliotropid biodiversity is connected with the large body of new knowledge of the contorted seafloor relief of the Indonesian region, it is clear that entire deep basins underlain by oceanic crust have never been sampled. The widespread occurrence of Cenozoic calliotropid gastropods in chemosynthetically based ecosystems is consistent with new data from petroleum exploration in the volcanic arcs of Indonesia documenting mud volcanoes and expulsion of geofluids (hydrocarbons, sulfides) that typically support rich microbial communities in the deep sea. The long and complex history of the collision of the Eurasian and Australian plates, arc volcanism, subduction, fusion of remnant pieces of continental crust, and opening of new deep gulfs affect the movement of shallow and deep currents and the Indonesian Throughflow from the Pacific into the Indian Ocean. This physical history generates testable hypotheses for reassessing the phylogenetic history of ancient gastropod lineages that originated in the Mesozoic Era or earlier.

Additional Keywords: Indonesia, Sulawesi, Wallacea, Indonesian Throughflow, plate collision, subduction, cold seep, chemosynthesis, intritacalx

INTRODUCTION

The Indo-West Pacific (IWP) region is recognized as the global center of marine biodiversity (Hoeksema, 2007;

Bellwood et al., 2012). Efforts to understand patterns of elevated diversity of the invertebrate biota have centered on a triangular region (the Coral Triangle) identified in the literature by more than 15 different descriptive terms (see Hoeksema, 2007). This same region has long been famous as a terrestrial biodiversity hotspot encompassing the thousands of tropical islands of eastern Indonesia. In the marine realm, modern research has concentrated on characterizing and explaining tropical shallow marine diversity. In gastropods, this has included the use of molecular tools to document patterns of speciation and dispersal and to investigate genetic connectivity and species boundaries (Reid et al., 2006; Williams et al., 2011; Williams et al., 2012).

There is increasing evidence of a more localized deep-water hotspot for basal gastropod diversity in the region of Wallacea, in marine basins underlain by oceanic crust between the shallow continental shelves of the colliding Australian, Eurasian, and Philippine tectonic plates (Hickman, 2009a, 2009b, 2009c, 2012). Anatomical and molecular investigations of this putative deep hotspot are impeded by lack of deep-water sampling and access to fresh material. However, emerging geological, geophysical and hydrographic understanding of remnant deep basins and deep forearc settings provides an unparalleled opportunity to study closely correlated patterns in marine geology, geophysics, and biology.

The primary purpose of this paper is to describe new species of narrowly endemic basal marine calliotropid gastropods in the Indo-West Pacific Region. A preceding paper (Hickman, 2012) described a new genus and two new species in the trochoidean family Gazidae Hickman and McLean, 1990, and will be followed by an account of new species in the seguenzioidean family Cataegidae McLean and Quinn, 1987.

Secondary objectives are to offer some new perspectives on persistent problems and challenges of calliotropid systematics and to present new perspectives on the tectonics and complex geologic history of the assembly of Wallacea and the specific deep tectono-sedimentary settings in which the new species were collected.

There are >100 available names for putative living species of *Calliotropis* Seguenza, 1903. Some species are narrowly endemic, but others have unusually broad ranges in which disjunct populations may be separated by thousands of kilometers. There is no satisfactory basis for morphological delimitation of subgenera, and a conservative treatment of new species is adopted here pending revisionary systematics integrating shell, anatomical, and radular characters with molecular sequence data. Most species currently are known only from shells, but the amount of unstudied material in museum collections is substantial. There are excellent species-level accounts for the Indo-Pacific (e.g., Vilvens, 2004; 2006; 2007) and the Philippines (Poppe et al., 2006) that include detailed geographic and bathymetric range data. An important compilation of data on the taxonomy and distribution of 245 South African vetigastropod species (Herbert, 2015) lends weight to a previously subjective and perplexing disjunction of taxa between the South African and Indonesian regions. New data from Late Cenozoic fossil vetigastropods in the Philippines (Helwerda et al., 2014) add to a new baseline for revisionary work. The following brief account of the history of calliotropid systematics provides a framework and rationale for the descriptions of new species.

NOMENCLATURE AND CLASSIFICATION OF LIVING CALLIOTROPIDS

Calliotropid gastropods are known primarily from exploring expeditions beginning in the late 19th and early 20th centuries, notably the CHALLENGER, VALDIVIA, INVESTIGATOR, TRAVAILLEUR, TALISMAN, SIBOGA, PRINCESSE-ALICE, LIGHTNING, PORCUPINE, BLAKE, and ALBATROSS. Species were described or treated under a variety of genus-group names, including *Trochus* (*Margarita*) (e.g., Watson, 1879; P. Fischer, 1882), *Solariella* (e.g., Wood-Mason and Alcock, 1891; Smith, 1894; Locard, 1897; Sowerby III, 1903), *Basilissa* (e.g., Dautzenberg and Fischer, 1897; Martens and Thiele, 1904), and *Solarielliopsis* (Schepman, 1908). Names were based exclusively on shell features until Schepman (1908) observed and figured both shell and radula (reproduced here as Figures 1–2) noting “how dangerous it is to classify such species without any knowledge of the soft parts.”

The nominotypical genus *Calliotropis* Seguenza, 1903 is based on a Pliocene-Pleistocene fossil species from Italy and is the name that has served for conservative treatments of more than 100 species from later deep-sea expeditions up until the present. Diagnosis of the family Calliotropidae Hickman and McLean, 1990 included features of the radula (Figures 3–4) that became clear with Scanning Electron Microscopy. They include a small-cusped “hooded” rachidian and large-cusped hooded lateral teeth with a system of deep interlocking basal projections and pockets, distinctive lateromarginal plates, extremely fine and numerous marginal teeth and peculiar mitten-shaped outermost marginal (Hickman

and McLean, 1990). An enlarged hindgut has been noted in many species along with evidence for selective deposit feeding (Hickman, 1981).

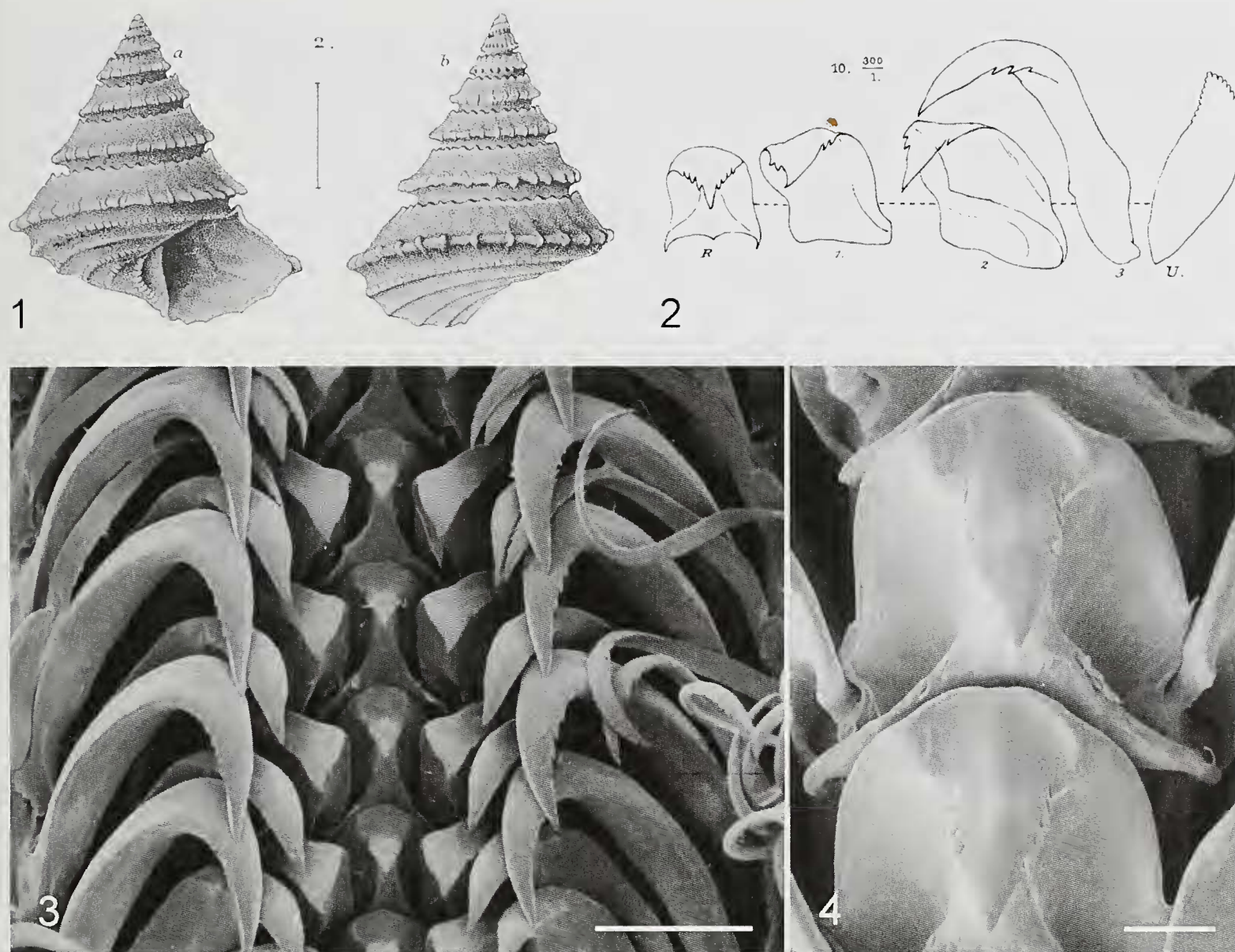
Other unique anatomical traits have been noted in calliotropids. The first is a large, enrolled, cylindrical elaboration of the right side of the male epipodium that has been interpreted as an “intromittent organ” (Dall, 1889) or “penis” or “copulatory organ” (Warén and Bouchet, 1989; Kano, 2007), or more conservatively as sperm delivery alternative to broadcast spawning that may not involve internal fertilization (Hickman, 1992; Kano, 2007). The second is the location of the “eyes” in some species at the bases of eyestalks and their modification to large irregular patches of black pigment (Dall, 1889). Observation of asymmetry and variability of the right and left pigmented regions has been interpreted as “a beginning of the loss of vision in an environment in which eyes are no longer of any use” (Warén and Bouchet, 1989). The asymmetry of the pigmented regions has been interpreted as evidence of separate genetic control of development of the right and left eye (Warén and Bouchet, 1989).

Twentieth century attempts to bring taxonomic order to *Calliotropis* include Marshall (1979) and Quinn (1979, 1991), although species have continued to be treated under inappropriate generic names (e.g., Abbott, 1974) or in inappropriate families (e.g., Nordsieck, 1968, 1982; Rubio and Rolan, 1987). A full review is beyond the scope of this paper.

Most significantly, the late 20th and early 21st century have seen a series of French deep-sea sampling expeditions recovering many calliotropids from bathyal depths in Oceania and the Indo-West Pacific Region. This work has further resulted in description of many new calliotropid species based exclusively on shell features (Poppe et al., 2006) and Vilvens, 2004, 2005, 2007) as well as new geographic and bathymetric records from the western Indian Ocean (Vilvens, 2006) and central Eastern Atlantic (Vilvens and Swinnen, 2008).

The monumental survey of Vilvens (2007) provides 251 figures of shells and classifies 94 species under *Calliotropis*, while declining to describe new subgenera or assign species to existing available genus-group names in the absence of anatomical data. Species are divided into 8 “formal groups” that are pragmatically justified and helpful for comparing shells of the same size and ratio of height to width. Descriptions and illustrations provide considerable additional detail such as numbers of cords on spire whorls and base, numbers of nodes or beads on spiral cords, whorl shape, and observations of ontogeny of these features.

Indonesia is the least well-sampled part of the Indo-Pacific Region. This is particularly unfortunate because it is geologically and hydrographically the most complex region on Earth and includes the Indonesian Through-flow (ITF) and the oceanic gateway connecting the Pacific and Indian Oceans (Tillinger, 2011). It is fortuitous that the Albatross Philippines Expedition of 1907–1910 included some exploratory deep dredging in



Figures 1–4. Calliotropid shell and radula. **1.** Schepman's original illustration of the shell of *Calliotropis pagodaformis*. **2.** Schepman's original drawing of the radula of *Calliotropis calcarata*. **3.** Scanning electron micrograph of the rachidian and lateral teeth from a typical calliotropid radula, scale bar = 100 µm. **4.** Detail of rachidian tooth cusp, shaft, hood and base, scale bar = 20 µm.

Indonesia (Sulawesi and Halmahera), and this paper documents six new calliotropid species from that expedition that have remained undescribed for >100 years. The paper also includes a new calliotropid species from the slope off eastern Australia and one from the eastern Andaman Sea.

NOMENCLATURE AND CLASSIFICATION OF FOSSIL CALLIOTROPIDS

A full review of the treatment of the fossil record of this group is not directly relevant to the description of new living species. However, there is a long history of using separate family-group names for Mesozoic and Cenozoic lineages that differ little in shell morphology. Hickman and McLean recognized Eucyclidae Koken, 1897 as an extinct, primarily Mesozoic, family group with maximum diversity in shallow seas of the Jurassic and introduced the new family group name Calliotropidae (as Callio-

tropini) for the Cenozoic radiation into deep water of taxa previously classified under a variety of inappropriate trochoidean family-group names. During the last ten years, paleontological treatments have introduced new family-group names and reallocated both fossil and living genera (e.g., Bandel, 2010), or advocated the use *Calliotropis* sensu stricto for the Cenozoic forms and using *Riselloidea* Cossmann, 1909 as a temporal subgenus for the Mesozoic forms (Ferrari et al., 2014). This may seem to be a highly unsettled systematic state. However, recognition of the seguenzioid affinities of many Mesozoic and Cenozoic taxa (Warén et al., 2003; Bouchet and Rocroi, 2005) has revolutionized systematics. Equally revolutionary is the increasing molecular support for a deep divergence and common ancestor of hypothesized seguenzioid radiations (Kano, 2007; Kano et al., 2009; Aktipis and Giribet, 2012), including those into the deep sea. *Calliotropis* is effectively a form genus at this stage, but it is poised for an interesting revision integrating many kinds of data.

Successful revision will require new anatomical and molecular data and extensive taxon sampling. In terms of shell morphology, it will require consistent definition of characters in terms of clearly differentiated character states. Size and shape terms, measurements, ratios, angles, whorl counts, counts of sculptural elements are useful for defining ranges of variation within species represented by many specimens. However, their value is *descriptive* rather than *diagnostic*. Several untapped sources of morphological hypotheses of relationships are identified in the species descriptions that follow. They include the recognition of terminal growth in the form of a thickened or reflected outer lip, a descending aperture, and modes of complete or partial closure of an open umbilicus. A columellar denticle is a terminal growth feature, if it is not a continuation of a columellar plication or denticulation of the columella present in earlier columellar ontogeny. Little attention has been paid to shell microstructure and to modes of decreasing shell thickness. Nacre that is incompletely obscured by an unusually thin veneer of outer shell, and fine microsculptural features on the outer shell are potentially important for defining clades within Calliotropidae. They also are potentially useful for evaluating sister-group relationships of seguenzioidean families. For example, closely spaced wavy, irregular, and sometimes bifurcating axial microstructure on the adult shell is expressed in different patterns in at least three seguenzioid families. Micrographs for calliotropids are figured as “wavy threads” by Marshall (1979) and for chilodontids as “scratch-like marks” by Herbert (2012). They are expressed in a similar pattern on cataegids (personal observation). This peculiar microsculpture is typically accompanied by different patterns of infill or overprint by intritacalx deposits that have not been characterized. Chalky or flakey, partially calcified exterior layers on the shells of some gastropod and bivalve taxa (D’Attilio and Radwin, 1971) are a form of remote biomineralization (*sensu* Hickman, 2013). Intritacalx takes on new taxonomic potential in terms of the untested hypothesis that it is produced by sulfate-reducing microbes (Vermeij, 2014).

MATERIALS AND METHODS

Locality data are given as they were originally reported at the time of collection and recorded in their respective museum data bases. Indonesian place names for ALBATROSS specimens use spellings in the U.S. Fish Commission Oceanographic Data Set and data on the original specimen labels, followed by parenthetical current names, translations and spellings. ALBATROSS depths are reported in fathoms, as they were originally recorded, followed by parenthetical conversions to meters. Acronyms for specimen repositories are: AMS: Australian Museum, Sydney; ANSP: Academy of Natural Sciences of Drexel University (formerly the Academy of Natural Sciences of Philadelphia), Philadelphia; USNM: National

Museum of Natural History, Smithsonian Institution, Washington, DC.

SYSTEMATICS

Subclass Vetigastropoda Salvini-Plawen, 1980
 Superfamily Seguenzioidea Verrill, 1884
 (Eucycloidea Koken, 1897, unranked)
 Family Calliotropidae Hickman and McLean, 1990

Genus *Calliotropis* Seguenza, 1903

Type Species: *Trochus otto* Philippi, 1844. Pliocene–Pleistocene, Italy, by original designation.

Calliotropis enantioserrata new species (Figures 5–11)

Diagnosis: Shell conical, 8 whorls, large for genus (height >25 mm), height exceeding width ($h/w = 1.2$) conical, with straight-sided whorls and broad, smooth sub-sutural ramp between two sharply serrate spiral cords; suture impressed in deep channel between adapical spiral with abapically pointed serrations and abapical spiral, on succeeding whorl, with adapically pointed serrations; umbilicus completely closed by reflexed columellar callus; aperture prosocline at 43° to axis of coiling, not descending, but outer lip with prominent reflected terminal thickening.

Description: Exterior shell layer thin, ivory-colored, smooth, lacking periostracum or continuous intritacalx that covers shells of some large calliotropid species. Fine microstriations and intritacalx visible with magnification. Nacre clearly visible through translucent exterior layer and refracts green and pinkish iridescence. In addition to two serrate spiral cords on each spire whorl, a third faintly denticulate spiral present, covered by suture throughout growth. Five fine, faintly denticulate spirals on convex shell base. An interior oblique prismatic layer (*sensu* Gainey and Wise, 1975) apparently lacking, and nacre not extending onto terminally thickened and reflected apertural lip of adult. Protoconch (Figure 9) translucent, with one smooth whorl and distinct boundary with opaque and ornamented early teleoconch.

Flattened and broadly triangular serrations pointing in opposite directions on either side of sutural channel (Figure 10). Surfaces of tooth-like serrations finely striate under magnification (Figure 11), and brown intritacalx most prominently developed within sutural channel (Figures 10–11).

Remarks: The new species is superficially similar to *Calliotropis excelsior* Vilvens, 2004, which also has flat-sided spire whorls and a suture located in a deeply excavated channel bordered on either side by prominent serrate spirals cords. However, *C. excelsior* has an open umbilicus and lacks a terminally thickened apertural lip. It is restricted in distribution to Fiji and New Caledonia,



Figures 5–11. *Calliotropis enantioserrata* new species. **5.** Semi-apertural, **6.** Apical, and **7.** Basal views of holotype, AMS C152225, height = 29.6 mm. **8.** Inclined abapical view of the spire of paratype, AMS C142224, height = 15.8 mm. **9.** Detail of protoconch, from Figure 8. **10, 11.** Details from Figure 9 of sutural channel, bordering rows of serrations, microsculpture and intritacalx.

disjunct from the new Australian species. Shell proportions of the holotypes of the two species are identical, although all specimens of *C. excelsior* are smaller (height <25 mm).

The flattened and broadly triangular serrations pointing in opposite directions on either side of the sutural channel (Figure 10) are one of the most distinctive features of *C. enantioserrata*. The opposing direction of the serrations on the cords bordering the sutural channel is also shared with some specimens that have been assigned to *Calliotropis pagodaformis* (Schepman, 1908), a species first described from southeastern Indonesia with a range that subsequently has been extended to the Solomon Islands (Vilvens, 2007). The holotype of *C. pagodaformis* (Figure 2) is distinctive in its narrower width and higher spire as well as the concave spire profile giving it a classically pagodaform appearance.

Type Material: Holotype, AMS C152225; height, 29.6 mm, maximum width 24.0 mm, from type locality; Paratype: AMS C152224, height 15.8 mm, maximum width 14.7 mm, R/V TONGAROA Station U222, 32°49.3' S, 152°49.1' E, off Newcastle, 1040–1075 m, 9 October 1982.

Type Locality: R/V TONGAROA Station U223, 32°58.8' S, 152°41.6' E, off Newcastle, New South Wales, 951–1150 m, 9 October 1982.

Other Material Examined: AMS C152228; a single small, broken and worn specimen from R/V TONGAROA Station U223, the type locality.

Distribution: Known only from two stations off Newcastle, New South Wales, Australia.

Etymology: Greek *enantios* (opposing) + Latin *serrata* (toothed edge), referring to the saw-like appearance of the spiral cords on either side of the channel between whorls and the opposing direction in which the flattened tooth-like projections point.

***Calliotropis andamanensis* new species**
(Figures 12–17)

Diagnosis: Shell conical, 8 whorls, moderately large (maximum height = 25 mm), width exceeding height ($h/w = 0.92$); spire profile straight-sided with three spiral cords; subsutural ramp broad and unornamented



Figures 12–17. *Calliotropis andamanensis* new species. **12.** Semi-apertural, **13.** Apical, and **14.** Basal views of holotype, ANSP 291376, height = 25.0 mm. **15.** Semi-apertural, **16.** Apical, and **17.** Basal views of paratype, ANSP 465552, height = 21.2 mm.

between adapical spiral and closely spaced pair of sharply nodose spirals connected by closely spaced, strongly sinuous axial threads; nodes most prominent on middle spiral and weak but more numerous on abapical spiral; suture closely following third abapical spiral on spire whorls; aperture strongly descending on body whorl; terminal lip flared and reflected, but not strongly thickened; umbilicus broad and deep, partially covered by reflected projection of parietal and columellar callus.

Description: Outer shell layer very thin, lacking periostracum and intritacalx. Ivory-colored, with nacre visible as a predominantly greenish refractive luster. Base (Figures 14, 17) weakly convex and predominantly smooth, with four to six smooth to faintly nodose spirals bordering umbilicus. Nodes most prominent on spiral immediately bordering umbilicus. Sinuous axial threads increasingly visible between pair of abapical spirals (Figures 12, 15), consisting of uniquely distinctive feature of the species. Teleoconch whorls with microstriations but lacking intritacalx. Prominent callus deposit divided into non-nacreous reflexed thickening that is only partially covered by a smaller tongue of nacre over umbilical portion (Figures 14, 17).

Remarks: This species is superficially similar to the species in “Formal group 4” of Vilvens (2007), which includes relatively large shells in which width exceeds height. Some of the species in this group have a similarly robust development of parietal and columellar callus that either partially or fully covers a broad umbilicus. However, none of these species have a descending aperture (Figures 12, 15), and they differ in whorl profile as well as the number and ornamentation of spirals on the spire and base.

The distinctive features of *C. andamanensis* are consonant with its hydrographic isolation.

Although the Andaman Sea is in the Indian Ocean, it is geologically a deep Sundaland basin, separated tectonically from shallow Indian Ocean floor by the Sunda Trench. At the same time, it is topographically and hydrographically separated from Indonesia and the deep basins of Wallacea by the shallow Sunda shelf. There is no significant connection between Wallacea and the Andaman sea via the narrow and shallow Malacca Strait between Sumatra and Malaysia. The Indonesian Throughflow of Pacific water into the Indian Ocean (the largest movement of ocean water on Earth) is via the Makassar Strait between Sulawesi and Kalimantan, entering the Indian Ocean between Lombok and Bali and through the Timor Passage to join the west-flowing South Equatorial Current.

Type Material: Holotype: ANSP 291376, height 25.0 mm, maximum width 27.3 mm; Paratype: ANSP 465552, height 21.2 mm, maximum width 26.8 mm. Both from type locality.

Type Locality: R/V ANTON BRUUN International Indian Ocean Expedition, Cruise 1, Station 17, 07°40' N, 97°08' E, Andaman sea, off Phuket Island, Thailand, 503–512 m, green-brown clay, 1963.

Distribution: Known only from the type locality in the Andaman Sea off Phuket, west Thailand.

Etymology: Named for the type locality.

***Calliotropis bukabukaensis* new species**
(Figures 18–22)

Diagnosis: Shell thin, conical, high-spired, and moderately large (height >15 mm), height exceeding width (height/width = 1.23); spire whorls stepped, with two sharply nodose spiral cords, suture impressed and slightly channeled above adapical spiral row of nodes; shoulder slope concave to slightly convex adapical to peripheral spiral cord with coarse nodes drawn out and connected; base with four thin, sharp spirals with concave interspaces ornamented with very fine axial lines; umbilicus broadly open, defined by finely beaded spiral and with fine axials on umbilical wall; columellar lip thickened and with prominent denticle extending into aperture.

Description: Nacre clearly visible through thin outer shell layer, remnants of thin, brownish-gold intritacalx present, best preserved on shell base and in umbilicus (Figures 20–22). Protoconch-teleoconch boundary not preserved on worn apex, but shell apparently with six or seven whorls. Aperture broken on all specimens, with no evidence of either thickened or descending apertural lip.

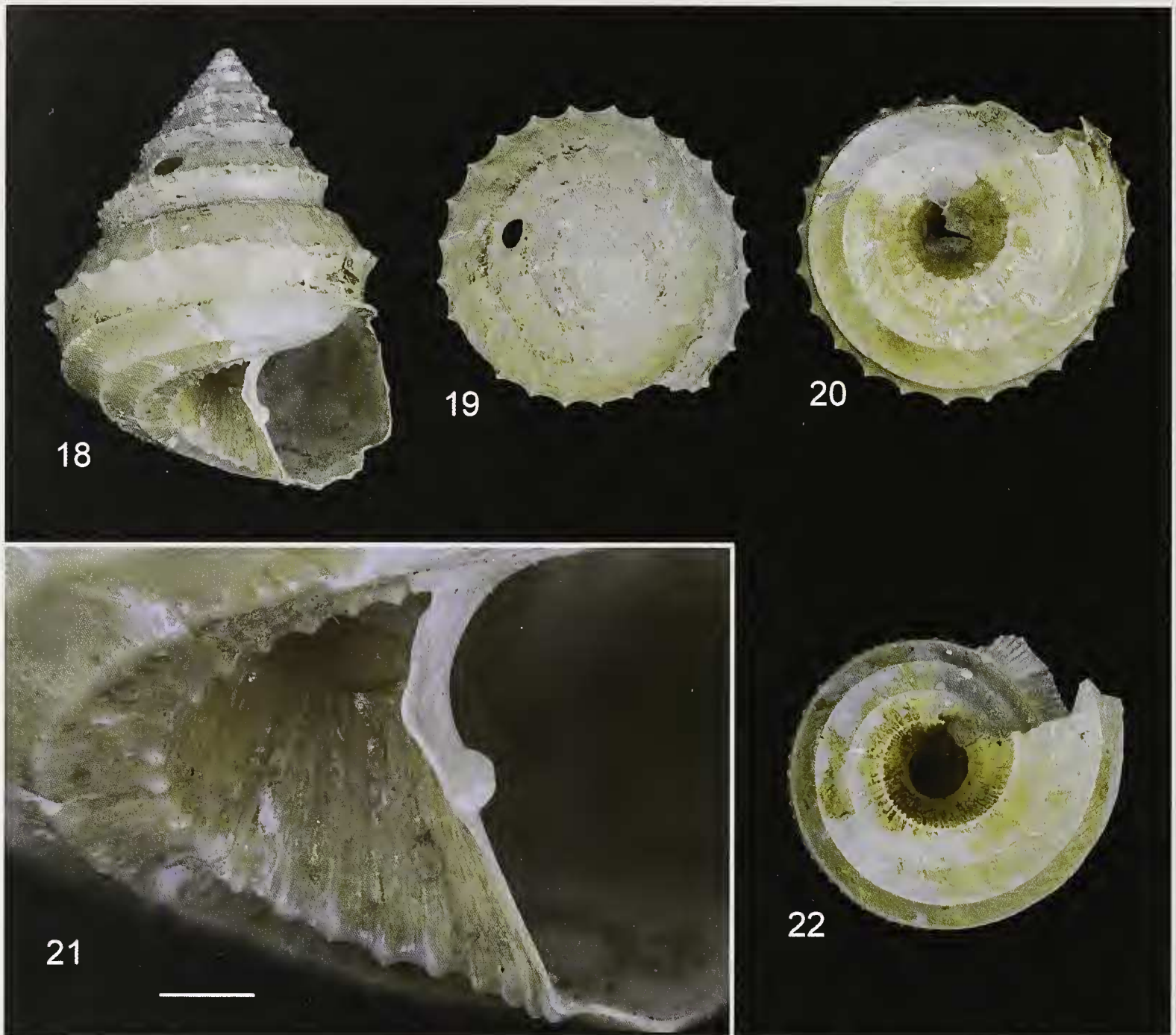
Umbilicus of holotype (Figure 20) partially blocked by thin, partially ruptured papery covering. This appears to have been formed by another organism, umbilicus of paratype (Figure 22) not similarly blocked.

Remarks: The new species is clearly distinguished from all previously described calliotropids by the very strongly developed, nodular columellar tooth (Figures 18, 21). Vilvens (2007) noted and illustrated (p. 42, figs 156, 158, and 160) a columellar tooth in three small-shelled species with depressed spires. In each of these species the denticle is considerably less well developed.

This is one of three new species recovered by the ALBATROSS in the Gulf of Tomini. It is easily distinguished from the large-shelled non-umbilicate species *C. tominiensis* and the smaller non-umbilicate *Calliotropis* new species?

Type Material: Holotype: USNM 239247, height 15.9 mm, maximum width 13.0 mm. Paratypes: USNM 1297170, height 12.5 mm, maximum width 11.3 mm; USNM 1409286, height 12.5 mm, maximum width 11.4 mm. All from type locality. Actual measurements are incomplete due to specimen breakages.

Type Locality: U.S. Fish Commission, R/V ALBATROSS, Station 5613, 00°42'00" N, 122°44'00" E, Gulf of Tomini,



Figures 18–22. *Calliotropis bukabukaensis* new species. **18.** Apertural, **19.** Apical, and **20.** Basal views of holotype, USNM 239247, height = 15.9 mm. **21.** Detail of the columellar tooth and umbilical microsculpture of holotype, scale bar = 1 mm. **22.** Basal view of paratype with unoccluded umbilicus, USNM 1297170, height = 12.5 mm.

Celebes (Sulawesi), Togian Islands S. of Buka Buka Island, 752 Fathoms (=1375 m), gray mud, 20 November 1909.

Distribution: Known only from the type locality.

Etymology: Named for the type locality.

***Calliotropis tominiensis* new species**
(Figures 23–25)

Diagnosis: Shell conical, 7 whorls, high-spired (spire angle = 58° , large (height >30 mm), height exceeding width (height/width = 1.31), spire whorls with one

prominent, nodose spiral cord; suture not impressed, closely following and almost completely covering second abapical spiral; base convex, with 4 finely beaded spiral cords; parietal and columellar callus reflexed, completely obscuring umbilicus and partially covering innermost basal spiral cord, aperture prosocline at 45° angle to axis of coiling; terminal lip thickened but not descending.

Description: Exterior shell layer extremely thin, with fine, closely spaced co-marginal lamellae and brownish-gold intritacalx well preserved on body whorl (Figure 23) and base (Figure 25). Outer layer eroded away on spire whorls (Figure 24) of holotype, exposing thicker nacreous layer that refracts predominantly green and pinkish



Figures 23–28. *Calliotropis tominiensis* new species and *C.* new species? **23.** semi-apertural, **24.** Apical, and **25.** Basal views of holotype of *C. tominiensis*, USNM 239217, height = 33.6 mm. **26.** Apertural, **27.** Apical and **28.** Basal views of figured specimen of *C.* new species, USNM 239216, height 15.7 mm.

iridescence (Figures 23–24). Inside aperture, nacre covered by very thin oblique prismatic layer that can be detected by touch—rougher toward interior and smoother toward apertural margin. Protoconch deeply eroded (Figure 24), and protoconch/teleoconch boundary not visible.

Remarks: There are very few species of *Calliotropis* that are as large and high-spined as *C. tominiensis*. *Calliotropis conoeides* Vilvens, 2007, known only from the Solomon Islands, is similar in size and proportions (h/w of the largest paratype = 1.3). However, the Solomon species lacks the terminally thickened outer lip. It also lacks the extensive parietal and columellar

callus that covers the umbilicus of *C. tominiensis*. *Calliotropis cynee* Vilvens, 2007 from the Tanimbar Islands, in the Banda Arc of southeastern Indonesia, is less than half the height of the new species and has a less elevated spire ($h/w \leq 1.24$). It also lacks the terminally thickened outer lip and extensive callus covering the umbilicus.

The biodiversity of the deep water basins of the Wallacean region of Indonesia is very poorly sampled, in contrast to the shallow waters of the region, which have been considered a crucible of species formation. Lack of sampling is unfortunate for two reasons. First, because of the megadiverse deep settings resulting from the complex and dynamic geological history of collisions, arc

volcanism, subduction, suturing of continental fragments, post-collision extension to form new deep embayments, and the topographic barriers to migration. Secondly, because the region offers hydrographically and geologically unique opportunities to sample very great depths very close to shore in isolated embayments and adjacent to numerous small islands.

It is fortunate that the ALBATROSS spent a brief time in Indonesia at the end of the 1907–1910 Philippine Expedition, and material dredged from the Gulf of Tomini and Gulf of Bone in Sulawesi provides a unique window on calliotropid biodiversity in two unusual tectonic settings. The significance of these settings is considered in greater detail in the discussion section.

Holotype: USNM 239217, height 33.6 mm, maximum width 25.7 mm.

Type Locality: U.S. Fish Commission, R/V ALBATROSS, Station 5606, 00°16'28" N, 121°33'30" E, Gulf of Tomini, Celebes (Sulawesi), Togian Islands S. of Dodepo Id., 834 Fathoms (=1525 m), green mud, 17 November 1909.

Distribution: Known only from the type locality.

Etymology: Named for the type locality.

***Calliotropis* new species**
(Figures 26–28)

Description and Remarks: An incomplete and worn shell recovered by the R/V ALBATROSS from >1000 meters in the Gulf of Tomini has a combination of characters that differentiate it from the five new Sulawesi species described herein. It is most similar to, and from the same station as, *C. tominiensis*. However, the peripheral spiral cord is prominently nodose and the shell is covered by an unusually heavy brown intritacalx with an exterior flaky layer in which there is imbedded sediment. The covering has adhered over most of the shell in spite of post-mortem corrosion and breakages (Figures 26–28). The spire angle is greater (67°), and the h/w ratio is less (1.1). The umbilicus is almost completely closed by parietal callus (Figure 28), and the columellar lip, which is not broken, is sharp rather than thickened and reflected as in the holotype of *C. tominiensis*. Additional material would be required to justify proposing a new name, and it is possible that the specimen is a juvenile of *C. tominiensis*. If umbilical closure is a terminal growth feature, this smaller specimen would have to be considered an adult.

Illustrated Specimen: USNM 239216, height 15.7 mm, maximum width 14.1 mm.

Locality: U.S. Fish Commission, R/V ALBATROSS, Station 5606, 00°16'28" N, 121°33'30" E, Gulf of Tomini, Celebes (Sulawesi), Togian Islands, S. of Dodepo Id., 834 Fathoms (=1525 m), green mud, 17 November 1909,

***Calliotropis tabakaensis* new species**
(Figures 29–31)

Diagnosis: Shell conical, 7 whorls, large (height \approx 17 mm), high spired (spire angle = 72°); spire moderately elevated with width and height almost equal (height/width = 0.9); spire whorls angularly convex, with two nodose spiral cords separated by concavity, suture shallowly impressed, following and barely covering fine, faintly beaded spire cord; adapical spiral on body whorl weaker with loss of nodes, peripheral spiral with 26 nodes; base weakly convex with four thin spirals that increase in width adapically, ornamented by slight swellings where crossed fine, sinuous axial threads; umbilicus open, aperture prosocline at 30° angle to axis of coiling; terminal lip thin and not descending.

Description: Protoconch of approximately one whorl, worn, boundary with teleoconch not clearly preserved (Figure 30). Outer shell layer thin, underlying nacre visible on entire shell surface. Intritacalx minimally developed and visible only under microscopic examination. Shell not encrusted during life or after death. Episodes of breakage and repair restricted to minor chipping of apertural lip.

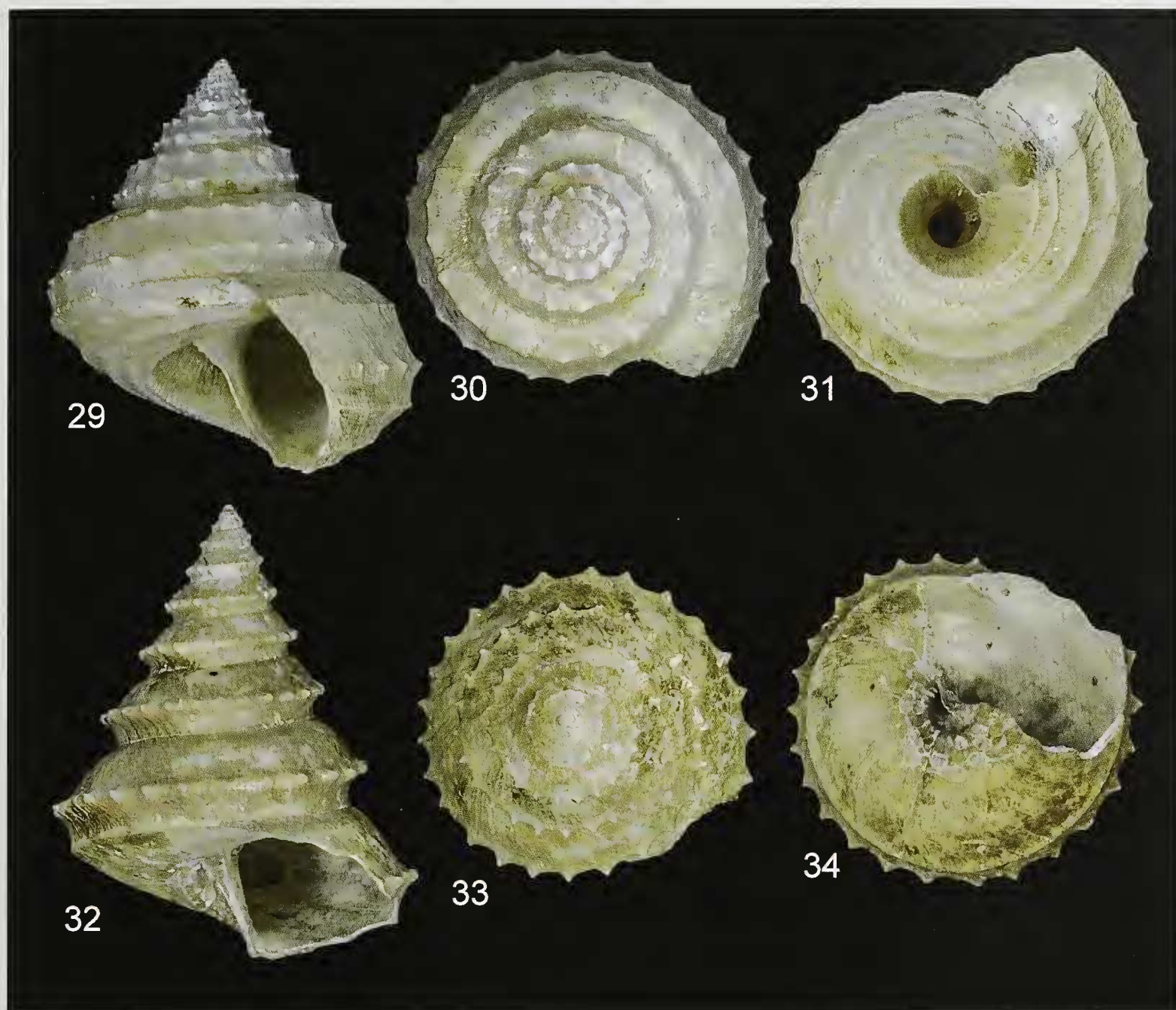
Remarks: In size and proportions the shell fits in Formal group 4 of Vilvens (2007) and is superficially similar to *Calliotropis debriosa* Vilvens, 2004, a species known from 9 stations in the southwestern Pacific from New Caledonia to Fiji and at comparable depths. The new species is distinguished by its extremely thin shell, stepped appearance of the rounded whorls, open umbilicus, two prominent nodose cords on the spire whorls, and the nearly equal ratio of height to width.

This is one of three new species from the Gulf of Bone. It is remarkable that the linear distance separating the type locality of *C. tabakaensis*, off the western margin of the southeast arm, from that of *C. locolocoensis*, off the eastern margin of the south arm is only 50 km. However, the shelf on either side of the gulf is exceptionally narrow and drops off rapidly to depths of 2000 m in the center of the basin. The basin itself is subdivided into fault-bounded sub-basins, and study of the deep-water marine molluscan fauna merits further sampling with the geology and hydrography in mind. A feature of the Gulf that is especially pertinent to the occurrence of large-shelled calliotropid gastropods is the presence of hydrocarbon seeps (Camplin and Hall, 2014).

Holotype: USNM 239445, height = 17.3 mm, maximum width = 17.4 mm.

Type Locality: U.S. Fish Commission, R/V ALBATROSS, Station 5655, 03°34'10" S, 120°50'30" E, Gulf of Boni (Bone), Celebes (Sulawesi), Buapinang, 3 miles off Cape Tabaka (Tobaku). 608 Fathoms (= 1112 m), green mud and fine sand, 18 December 1909.

Distribution: Known only from the type locality.



Figures 29–34. *Calliotropis tabakaensis* new species and *C. locolocoensis* new species. **29.** Semi-apertural, **30.** Apical and **31.** Basal views of holotype of *C. tabakaensis*, USNM 239445, height = 17.3 mm. **32.** Apertural, **33.** Apical and **34.** Basal views of holotype of *C. locolocoensis*, USNM 245478, height = 18.2 mm.

Etymology: Named for the type locality.

***Calliotropis locolocoensis* new species**
(Figures 32–34)

Diagnosis: Shell conical, 9 whorls, unusually slender and high-spined (spire angle = 55°), large (height >15 mm), height exceeding width (height/width = 1.23); spire whorls with one bluntly spinose, keel-like spiral cord; base shallowly convex and smooth, bordered adapically by unornamented spiral; umbilicus almost completely covered by reflexed columellar and parietal callus and bordered by two faintly nodose spiral cords; outer shell layer covered by thin but continuous tan-colored intritacalx,

thicker inner nacreous layer visible through the outer shell layer where intritacalx has eroded away.

Description: Outer lip of holotype broken, but the trace of the break indicates that the final lip was not descending. Throughout ontogeny, it followed and covered the unornamented spiral defining the break between the spire and the base of the shell. The protoconch is approximately one whorl and worn so that the protoconch-teleoconch boundary is indistinct.

Remarks: In size and general appearance there is a close, but superficial, resemblance to *C. pagodaformis* (Schepman, 1908), originally described under *Solar-ielliopsis* Schepman, 1908 for inclusion of 11 deep-water

Indonesian species. Schepman based the genus on *S. calcarata* recognizing that his type species had a radula (Figure 2) distinct from that of *Solariella* Wood, 1842. Although he had no radular data for the other ten forms that he placed in *Solarielliopsis*, he emphasized (p. 53) "how dangerous it is to classify such species, without any knowledge of the soft parts."

Schepman's original figure of the shell of *C. pagodaformis* is reproduced above (Figure 1) for comparison with *C. locolocoensis*. The spire whorls of the new species have a single beaded spiral at the periphery and lack the subsutural spiral with adapically directed spines. The suture is not in a channel, and the shoulder slope is slightly convex rather than flat. The base lacks distinct spiral cords, and the columella is slightly prosocline rather than coincident with the axis of coiling.

There are prominent plate tectonic and hydrographic barriers separating the superficially similar pagodaform species in Indonesia. Schepman's localities from the Siboga Expedition were in the Outer Banda Arc thrust belt of eastern Indonesia, whereas the Albatross station is in deep water very close to shore in the Gulf of Bone in Sulawesi. The gulf is a complex, post-collision, extensional basin, emptying to the south into the Flores Sea. The gulf opened during the Neogene to separate the

south and southeast arms of Sulawesi (Sudarmono, 2000; Camplin and Hall, 2014). Four Indonesian localities from which *C. pagodaformis* has been collected more recently (March, 1990) and reported by Vilvens (2007, p. 7) are also in the Banda Arc (Tanimbar Islands), tectonically in the collision zone between the Australian continental margin and the Banda volcanic Arc above the Timor trough (Barber et al, 1986). The three new species described here from the Gulf of Bone may reflect its isolation and separate geologic history.

Holotype: USNM 245478. Height 18.2 mm, maximum width 14.8 mm.

Type Locality: U.S. Fish Commission, R/V ALBATROSS, Station 5658, 03°32'40" S, 120°31'30" E, Gulf of Boni (Bone), Celebes (Sulawesi), off Loko Loko (Locoloco), 510 Fms. (=933 m), gray mud, 19 December 1909.

Distribution: Known only from the type locality.

Etymology: Named for the type locality.

***Calliotropis lamuluensis* new species**
(Figures 35–37)



Figures 35–40. *Calliotropis lamuluensis* new species and *C. glypta* (Watson, 1879). 35. Semi-apertural, 36. Apical and 37. Basal views of holotype of *C. lamuluensis*, USNM 239424, height = 19.4 mm. 38. Semi-apertural, 39. Apical and 40. Basal views of a hypotype of *C. glypta*, AMS C.115685, height = 17.2 mm.

Diagnosis: Shell broadly conical, 6 whorls, low spired (spire angle = 90° , large (height ≈ 20 mm), width exceeding height (height/width = 0.84); spire whorls weakly convex, with two (increasing by intercalation to three) nodose spiral cords; suture shallowly impressed beneath and following abapical spiral; body whorl with three coarsely nodose spirals on shoulder slope (30, 34 and 38 nodes from adapical to abapical spiral on body whorl), peripheral spiral more finely nodose (65 nodes on body whorl); base weakly convex with seven sharply nodose spirals that become increasingly wide and more distinctively nodose abapically; parietal and columellar callus strongly reflected and completely covering umbilicus; aperture strongly prosocline at 43° angle to axis of coiling, terminal lip very slightly thickened but not descending.

Description: Apertural lip of holotype chipped, four roughly circular attachments scars (Figure 36) present on body whorl made by an epizoan no longer present. Two major and several minor episodes of shell breakage and repair during growth. Periostracum not present. Fine, sinuous and prosocline axial “scratch-marks” on shell interspersed with minimally developed intritacalx. Protoconch and earliest portion of teleoconch broken, nacre visible in several places where very thin exterior shell layer is broken or eroded away. Nacre in interior of aperture covered, but visible through a thin oblique prismatic layer that is a characteristic feature of many large calliotropid shells. Nacreous layer in this species thicker than in most large calliotropids, giving shell a more robust appearance.

Remarks: *Calliotropis lamuluensis* differs dramatically in shell thickness, proportions, and many discrete features from the two new species described from farther within the gulf. As noted above, this may reflect isolation tied to the complex tectonic history and opening of the gulf (Sudarmono, 2000; Camplin and Hall, 2014). In view of the complex geology and hydrography and the hydrocarbon seepage reported in the Gulf (discussed above) these locations would profit from further sampling of the deep-water marine molluscan fauna.

The new species is closest in size, proportions, and ornamentation to the species in Formal group 4 of Vilvens (2007). It has the lowest h/w ratio of any of the species in the group and differs from these openly umbilicate shells in having a fully reflexed umbilical closure (Figure 37). It also differs from group 4 species in having a thicker shell. An Australian specimen of *Calliotropis glypta* (Watson, 1879), is illustrated here for comparison (Figures 38–40). Thickness of the basal portion of the apertural lip is 0.4 mm, in contrast to 0.7 mm for *C. lamuluensis*. Shells of both species supported encrusting epizoans to a greater extent than typical in other calliotropids.

Holotype: USNM 239424, height = 19.4 mm, maximum width = 23.1 mm.

Type Locality: U.S. Fish Commission, R/V ALBATROSS, Station 5650, $4^\circ 53' 45''$ S, $121^\circ 29' 00''$ E, Gulf of Boni (Bone), Celebese (Sulawesi), Buapinang, off Lamulu Point, 540 Fathoms (=988 m), green mud, 17 December 1909.

Distribution: Known only from the type locality.

Etymology: Named for the type locality.

DISCUSSION

The new species described above shift the center of diversity of large-shelled (height > 15 mm) calliotropids into the tectonically and hydrographically complex Wallacean region of Indonesia, with its long history of plate collisions, subduction, and volcanic arc volcanism. They also shift peak diversity of large-shelled calliotropids to depths exceeding 1000 m. This is remarkable because the deep-water fauna of Indonesia is still undersampled. A previous paper (Hickman, 2012) provides additional background on the unique ecologic, biogeographic, and geologic aspects of Wallacean deep diversity.

A simplified map of deep Wallacea (Figure 41) shows the localities of the species described above and provides a frame of reference for the following discussion of patterns of narrow endemism, disjunction, and relictual accumulation of taxa.

The calliotropid species are spatially distributed in geologic settings that include tectonically isolated deep-water basins underlain by oceanic crust. In one interpretation (Lee and McCabe, 1986) the Sulu, Celebese, and Banda seas are characterized as remnants of a large Cretaceous–Eocene seaway. Tectonic elements of Wallacea include major forearc subduction complexes, fusions of colliding microplates, shifting plate boundaries, and formation of narrow gulfs and extensional basins opening by rollback at subduction hinges. The Molucca Sea is unique—the only modern example of double subduction at the collision of two facing volcanic arcs, eliminating an entire oceanic plate and trapped Indian Ocean lithosphere (McCaffrey et al., 1980; Hall, 2006; Hall and Smyth, 2008). This is the first recognition of the relictual deep-water fauna in a setting that has heretofore been of intense interest only to geologists.

The corresponding sedimentary and geochemical settings associated with the complex geologic history of marine Wallacea are consistent with the development of unusual deep marine communities. Convergent plate margins frequently are sites of expulsion of squeezed percolating fluids containing sulfides and hydrocarbons (oil, gas, and methane hydrates). These fluids feed microbial productivity and development of chemosymbiotically based food chains. Although such settings are typically not good candidates for the formation of large petroleum reservoirs, ongoing investigations of petroleum potential in Indonesia have revealed the presence of discrete hydrocarbon seeps, mud volcanoes and explosive methane release (Barber et al., 2000; Sudarmono, 2000; Charlton,

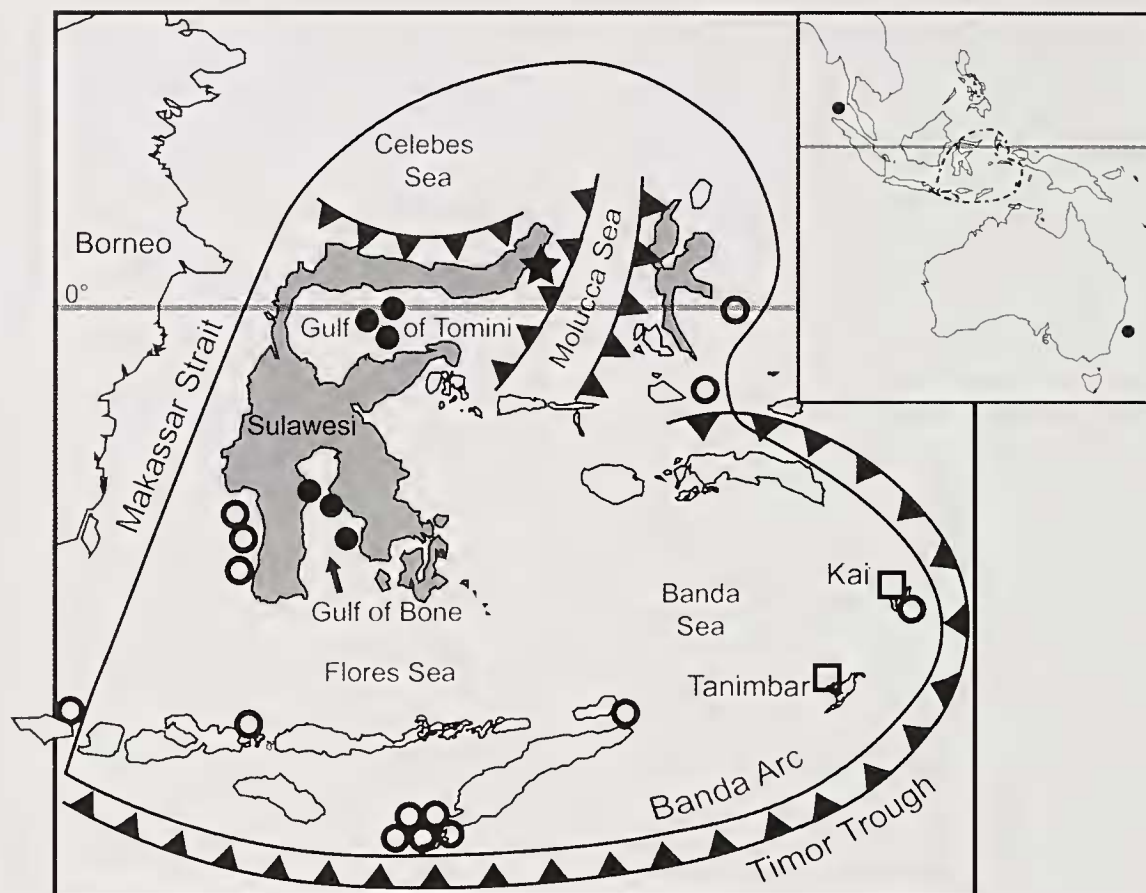


Figure 41. Simplified map of the deep Wallacean region of the Indonesian Archipelago with localities for the new calliotropid species (solid circles) and previously described calliotropids from the Siboga Expedition (open circles) and French KARUBAR Expedition (open squares). The locality of the previously described new gazid genus and species is shown by a solid star. Isolated occurrences in deep-deep-sea basins, gulfs and straits are depicted in the context of primary zones of collision and subduction (solid lines with triangular tick marks) and associated volcanic arcs at plate boundaries where subduction has occurred or is occurring.

2004; Jablonski et al., 2007; Camplin and Hall, 2014) as well as sediment systems with diffusive methane emission and a deep biosphere of chemosymbiotic microbial communities (Schipper et al., 2010; Siegert et al., 2011).

RELATIONSHIP OF SHALLOW AND DEEP BIOGEOGRAPHIC PATTERNS

The patterns and explanations of deep-water biodiversity and connectivity in Indonesia are highly unlikely to correspond with those that have begun to emerge for shallow water taxa. In shallow-water taxa there is a striking disconnect between surface currents and routes of gene flow (e.g., Benzie, 1998, 1999; Benzie and Williams, 1995, 1997; DeBoer et al., 2008), perhaps related to underestimation of the importance of seasonal cycles in the upper-ocean mixed layer in which monsoonal forcing generates reversals in flow directions (Lindstrom et al., 1987; McCreary et al., 2001). Current directions and flow speeds are notably different in deep water. Sills between deep basins impede flow, and the vetigastropod taxa under consideration here lack the feeding planktonic larvae that enhance the dispersal potential of many shallow-water taxa. Deep-water diversity is likewise

unaffected by the diversity increase in reef-associated habitats and the Oligo-Miocene pulse of shallow-water diversification of reef-associated taxa in the Indo-West Pacific (Williams and Duda, 2008).

In fact, it is argued here that modern marine biogeographic patterns in the Indonesian region cannot be understood apart from geologic history. Reconstruction of the entire Cenozoic history of plate boundaries (Hall, 2001, 2002), especially the dramatic effects of episodic volcanic arc processes on marine topography (Hall and Smyth, 2008), argue against simplistic inferences of marine connectivity and historical biogeography based solely on present configurations.

EXPLAINING DISJUNCT DEEP-WATER TAXA IN WALLACEA AND SOUTHERN AFRICA

The disjunct distribution of calliotropid species in deep Pacific waters of Wallacean Indonesia and the far western Indian Ocean has been recognized for more than 100 Years. Schepman (1908) reported *Calliotropis metallica* (Wood-Mason and Alcock, 1891) from four stations in Indonesia. The species is better known from Madagascar and southern Africa, and was described

originally from the Gulf of Mannar in the Indian Ocean. *Calliotropis buccina* Vilvens, 2006, described from Reunion Island in the southwestern Indian Ocean is now reported from the Kai archipelago in southeastern Indonesia as well as the Solomon Islands, adding a third disjunct element (Vilvens, 2007). This peculiar pattern is not restricted to calliotropid gastropods, although it does appear to occur in lineages with a long, pre-Cenozoic geologic history. It is consistent with the hypothesis that these are relictual occurrences of taxa and lineages with ranges that have been fragmented and reduced. Two additional examples are given here.

ABYSSOCHRYSID GASTROPODS

The first is in the distribution of living species of the aeonogastropod family Abyssochrysidae Tomlin, 1927. In a revision of the genus, Houbriek (1979) provided a detailed analysis of the shell morphology, anatomy, and radulae of the two living species: one described by Tomlin (1927) from 1645–1828 m off the Cape of Good Hope and the other described by Schepman (1909) from the Sulu Sea in Indonesia. Based on further examination of hydrographic data and search of the fossil record, Houbriek (1979) proposed that these two living abyssochrysid are deep-water relicts of the Paleozoic-Mesozoic superfamily Loxonematoidea (Koken, 1889). Although Houbriek (p. 1) considered his proposal to be “radical”, description of new material from deep-sea expeditions (Bouchet, 1991) recognized five species, including a new species from the Makassar Strait in Indonesia and a distribution that is localized in the deep-water settings around Sulawesi.

The Indonesian material examined by Houbriek (1979) included specimens from the ALBATROSS expedition, and it is interesting to note that one of the specimens appears to be from the same locality in the Gulf of Bone as the type of the *Calliotropis* species described above as *C. lamuluensis*. Houbriek did not give the station number or coordinates, but the reported depth is the same as well as the location off Lamulu Point.

Description of a putative abyssochrysid from the middle Eocene of the northwestern Olympic Peninsula in western Washington (Goedert and Kaler, 1996; Kiel, 2008) adds a new paleoenvironmental dimension to the post-Mesozoic disjunct geographic distribution. The Eocene species is known from >50 specimens in a localized methane-derived authigenic carbonate deposit in association with chemosymbiotic solemyid, lucinid, thyasirid, and vesicomyid bivalves as well as abundant serpulid and vestimentiferan worm tubes.

LIVING COELACANTHS

The same pattern of disjunction is not confined to marine invertebrates. It has received considerable attention with discovery of a second population of the “living fossil” coelacanth genus *Latimeria* off Manado, Sulawesi, Indonesia

(Erdmann et al., 1998). The Sulawesi population is separated by a distance of >10,000 km from the African population in the Comoros Islands (see Springer, 1999; Holder et al., 1999). Although the two populations must share a common ancestor, there is no available evidence to test alternative historical biogeographic hypotheses.

CONCLUSIONS

Knowledge of the internal phylogenetic structure of Calliotropidae is highly unsatisfactory, although the anatomical, and molecular data are consistent with placement of Calliotropidae in Seguenzioidea. For most of the living species and available genus-group names there are no anatomical or molecular data and no consistent terminology for shell features. There are no published accounts of the behavior of live animals and little information on habitats aside from records of some large-shelled deposit-feeding species with enlarged hindguts in hydrocarbon seep biotopes where primary productivity is greatly enhanced by microbial chemosynthesis. Problems are compounded by the long fossil record and history of paleontological treatments using separate names and classification.

On the positive side, resurgence of interest in deep-sea exploration and use of new sampling methods are adding considerably to the amount of new material available for study. In addition, there seems to be increased interest in describing older material that has been languishing in museum collections. New techniques enable illustration of microsculpture and features that have not been noted previously. This paper draws special attention to the potential of new characters for diagnosing taxa.

The discovery of elevated deep-water diversity of calliotropid gastropods in the Indo-West Pacific, especially in the deep basins in the Wallacean region of Indonesia, should not be surprising in view of new data on regional tectonic history: collision of the Australian, Eurasian, and Philippine Sea plates; development of volcanic island arcs; arc-arc and arc-continent collisions; subduction; deformation, faulting, rotations and translations; openings and closings of distinct deep-water basins, gulfs and straits; and the movement and accretion of microplates. Evolutionary persistence of Indian Ocean faunal elements in Wallacea is not a difficult fate to imagine for taxa arriving on Indian Ocean lithosphere trapped and ultimately subducted in the collision zone.

New understanding of seafloor topography and hydrography of the Indo-West Pacific is in turn related to the shallow and deep-water current systems that affect biogeographic patterns. History and physical oceanography of Indonesian Throughflow and the gateway connection between the Pacific and Indian Oceans is potentially a strong key to understanding some of the puzzling biogeographic connections between southern Africa and Indonesia.

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